Species Richness: Small Scale

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Advanced article

Article Contents

doi: 10.1002/9780470015902.a0020488

Species richness, defined as the number of species per unit area, is perhaps the simplest measure of biodiversity. Understanding the factors that affect and are affected by small-scale species richness is fundamental to community ecology.

Introduction

The ability to measure biodiversity is critically important, given the soaring rates of species extinction and human alteration of natural habitats. Perhaps the simplest and most frequently used measure of biological diversity is species richness, the number of species per unit area. A vast amount of ecological research has been undertaken using species richness as a measure to understand what affects, and what is affected by, biodiversity. At the small scale, species richness is generally used as a measure of diversity within a single ecological community, habitat or microhabitat, although the definition of small depends on the species in question.

Ecologists have long been intrigued by the fact that small-scale species richness can vary substantially among communities. The factors related to these patterns of small-scale species richness include (1) geographic factors such as scale of observation, available species pool and dispersal patterns, (2) biotic factors such as competition or predation and (3) abiotic environmental factors such as site resource availability, disturbance and physical conditions.

Ecologists have also studied whether changing small-scale species richness might impact the functioning of communities through modification of such attributes as productivity, stability and invasibility. Although many of the studies about small-scale species richness have focused on sessile organisms such as plants or barnacles, there are also studies that incorporate mobile organisms such as arthropods; much of the theory about this topic can be applied to both.

Factors that Affect Species Richness

Geographic factors

Spatial definitions of diversity based on species richness

Species richness is simply the number of species per unit of area, while biological diversity is a broader term that can incorporate functional group diversity, number of trophic levels or relative species abundance. For example, the diversity indices of Simpson and Shannon incorporate species abundances in addition to species richness and are intended to reflect the likelihood that two individuals taken at random are of the same species. However, they tend to de-emphasize uncommon species.

Species richness measures are typically separated into measures of α, β and γ diversity (Whittaker, 1972). α Diversity (also referred to as local or site diversity) is nearly synonymous with small-scale species richness; it is measured at the local scale and consists of a count of species within a relatively homogeneous area. From a practical standpoint, the determination of what is local and homogeneous depends on the size of the organisms being studied, and could range from a 1 m^2 sample of grassland herbs to a 1000 m^2 stand of trees or a 1 L plankton sample.

β Diversity is the change in species composition from one site to the next along a gradient, also referred to as species turnover. Unlike α diversity, which provides information about diversity at a local site, β diversity provides information about how diversity changes along environmental gradients.

Finally, γ diversity is a measure of the diversity across habitats or community types within a landscape or region. While α diversity usually refers to a homogeneous area, γ diversity includes the various habitats, conditions and communities. Because γ diversity is defined as the product of α and β diversity, it takes into account both the local richness (α diversity) of sites within the region as well as the rate of change in richness between those sites (β diversity), to give a measure of richness that reflects diversity across the communities and conditions within the geographic region.

Species–area relationships

The change in species richness with spatial scale can be shown using species–area curves where species richness is plotted on the y axis against area on the x axis (**Figure 1**), often with both richness and area expressed on a logarithmic scale. Comparisons of how species richness varies across scales can be more informative than comparisons at a single scale. A single measurement of species richness taken at a very small scale may mislead a researcher into believing that a site has low diversity when it is in fact

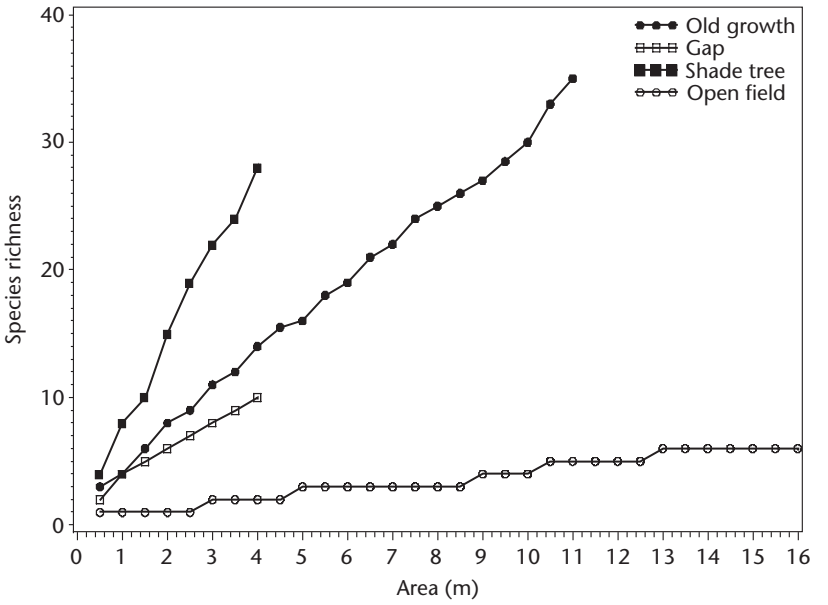

Figure 1 Species–area curves for four habitats, Las Cruces, Costa Rica, showing different rates of species accumulation in old-growth forest, a forest gap, an open field and under a shade tree in the open field (data from Rebecca Brown).

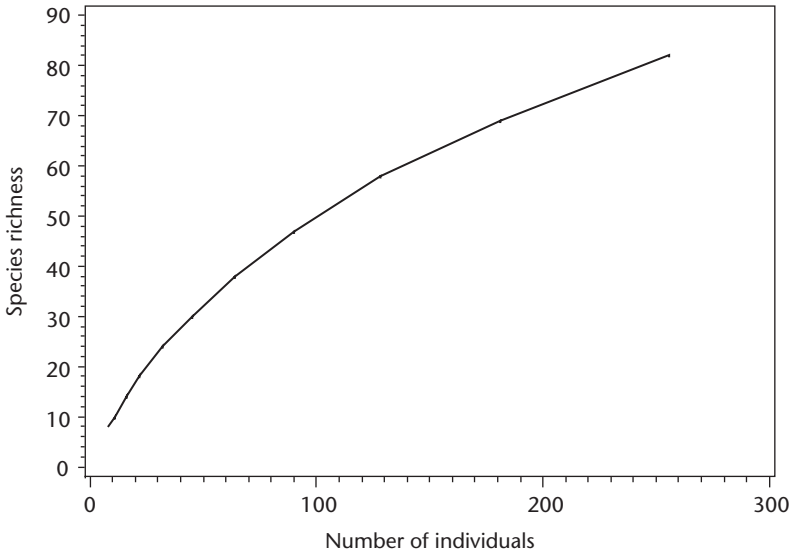

Figure 2 Species–individual curve for old-growth forest habitat, Las Cruces, Costa Rica (data from Rebecca Brown).

relatively rich at larger scales. This is because the processes that determine richness are likely to change with scale. For example, the slope may be influenced by an increase in habitat diversity resulting from sampling a larger area. Moreover, a sampling effect due to a larger area having more individuals and thus a greater proportion of the species pool (i.e. more individuals and thus more species; Connor and McCoy, 1979) is likely to depress diversity at very small scales, but not at somewhat larger scales (Fridley *et al*., 2006). Species–individual curves, which assess species diversity by comparing rates of new species addition (y axis) with increasing numbers of individuals (x axis), have been used to assess the relative contribution of sampling effects (**Figure 2**). These have been particularly useful in measuring tree diversity in tropical rainforests (Condit *et al*., 1996) where tree size is so large that it can be difficult to sample a reasonable proportion of the species pool.

The species pool and its effects on small-scale species richness

The 'species pool' concept is generally used to refer to the number of species adapted to a site that are available to

colonize that site (Eriksson, 1993). Pärtel *et al*. (1996) further distinguished between regional, local and actual species pools. They define the regional species pool as the subset of all the species in the region (or subset of the γ diversity) that could potentially coexist in a given habitat type. The local species pool is the set of species occurring in a local landscape type (such as a watershed) that could coexist in the habitat. For example, for Ponderosa pine habitat, the region might include most of the Rocky Mountains in the western United States whereas local might refer to the watershed of the Salmon River in Idaho. Presumably, constituents from the local species pool could more easily migrate to a given site than species from throughout the regional species pool. The actual species pool (or the community species pool, as per Zobel *et al*., 1998) represents the set of species present within a contiguous section of the target habitat. This section of habitat represents what ecologists refer to as a community, which is generally defined as an association of interacting populations within a given area. Small-scale species richness is, therefore, the portion of the actual species pool that ends up in a subsample of the community measured over some unit of area. In areas with a larger regional, local and actual species pool, one might therefore expect higher levels of small-scale species richness. **See also**: Community Ecology: An Introduction

The composition of the regional species pool depends on factors such as rates of evolution and environmental constraints. Dispersal limitation may prevent some species in the regional pool from being in a local species pool. For example, if the local area is an island or an isolated watershed, species in the regional pool may be missing simply because they cannot get there. Dispersal limitation along with various biotic and abiotic filters can affect the difference in species composition between the local and actual species pools and thus the potential species richness of a plot. For example, strong interspecific competition may serve as a filter, preventing species from colonizing a site even though they could otherwise persist there (Zobel *et al*., 1998).

One of the difficulties with using the species pool concept to understand small-scale species richness is that it can be very difficult in practice to determine what species should be included in the regional, local and actual species pools. For example, it can be difficult to determine what portion of the species in a region could potentially persist in any given site. For the actual species pool it can be difficult and arbitrary in practice to assign the edge of a community, especially for sites where communities gradually change across some gradient.

Immigration

Immigration and extinction processes are shaped by geographic factors, such as distance between habitat patches, as well as biological factors, such as viable population size. Because immigration is often treated within the field of biogeography, it is included here as a geographic factor despite the fact that it is also a biological process.

The Theory of Island Biogeography, developed by MacArthur and Wilson (1967), suggests that species richness represents an equilibrium between immigration and extinction processes affecting a community. High levels of immigration cause species richness to be high, whereas high levels of extinction cause richness to be low. Using islands as a model, MacArthur and Wilson suggested that distance from the mainland controls immigration rates with closer islands having higher rates of immigration, while island size controls extinction rates with smaller islands having higher rates of extinction owing to small population sizes. Simberloff and Wilson (1970) tested this model in a classic experiment using different sized mangrove islands at different distances from the mainland in the Florida Keys. They fumigated arthropod species on the islands, and observed that patterns of recolonization over two years matched the predictions of the equilibrium theory. Although MacArthur and Wilson did not explicitly specify what might affect rates of extinction or immigration, their theory provides a unifying framework for understanding how the balance between widely different processes can affect species richness. **See also**: Islands

In MacArthur and Wilson's theory, immigration is one of the major drivers of local species richness. Immigration, often referred to as colonization, involves two components: the dispersal of new species into a site and their establishment within that site. The rate of dispersal of propagules into a site is referred to as propagule pressure. When propagule pressure is particularly high, species richness can be increased in a site by the presence of transient species that would not otherwise persist there owing to insufficient reproduction, a phenomenon referred as a spatial mass effect (Shmida and Wilson, 1985). In contrast, recruitment limitation refers to the situation where there are too few propagules to fill all of the available niches (Victor, 1986). Recruitment limitation has been invoked as an explanation for the high species richness of tropical rainforests (Hubbell *et al*., 1999), where tree seedling recruitment is often so low that competition among seedlings does not limit survival to the few most competitive species. Recruitment limitation can also reduce species richness if there are few species available to colonize a site. The study of supply-side ecology (Roughgarden *et al*., 1985) elaborates on the role that recruitment limitation plays in driving the species richness and composition of communities. Supply-side ecology seeks to explain why in some sites, such as highly disturbed rocky intertidal habitats, species richness and composition of sessile intertidal organisms such as red algae are driven more by factors that affect the pool of propagules arriving at the site than by species interactions, such as competition.

Biological factors that affect species richness

Competition

Competitive exclusion, perhaps the most often cited form of species interaction in ecology, occurs when one species

excludes a second because of greater ability to capture resources for growth and reproduction. The importance of competition for resources has led some to wonder how so many species can occur in such small areas (Hutchinson, 1959). If competitive exclusion predicts one species eliminating another from a site, what explains the coexistence of species we so often observe?

Tilman (1982) provides one solution to the problem presented by competitive exclusion. He proposed that species are able to coexist due to tradeoffs in relative resource needs. His model is based on the idea that different species draw down particular nutrients at different rates. Depending on the initial conditions, each species can reduce the nutrient that limits it to the point that each species is held in check by nutrient limitation, but because the species are limited by different nutrients, they can coexist. If there is small-scale environmental variation in resource availability, then the conditions for many pairs of coexisting species might occur in close proximity.

Numerous authors have observed that the relationship between productivity (measured as biomass accumulation) and species richness tends to be unimodal, with species richness peaking at intermediate levels of productivity (Grace and Jutila, 1999). Where productivity is very low few species can persist, and where productivity is very high a small number seem to win at competition, but at intermediate levels many coexist.

Peet and Christensen (1988) suggested that the mechanism for the unimodal relationship between productivity and small-scale richness can be found in the change in character of competition across a fertility gradient. At low levels of fertility, competition is symmetric in the sense that ability to capture resources is proportional to size (essentially, root surface area). However, at high levels of fertility, the larger individuals can overtop and preempt light from the smaller ones with the result that competition becomes asymmetric with the larger individuals capturing a disproportionate share of the resources. The most species-rich plant communities at scales on the order of 1 m^2 are infertile grasslands (sometimes with in excess of 40 species of plants per square metre) that are subject to chronic disturbance from some factor such as mowing, grazing or fire that removes the tops of the plants on a regular basis, reducing the degree of competition for light (asymmetry of competition) and allowing high species richness to occur on more fertile sites than would be the case in the absence of such disturbance. Similarly, the peak in richness on the fertility gradient occurs on much higher fertility sites in woodlands than grasslands because the available light in the forest understory is substantially reduced with the consequence that more nutrients are needed to achieve sufficient growth for asymmetric competition to occur (see Graves *et al*., 2006). This also explains why an increase in productivity beyond some threshold (such as from the addition of fertilizers) can negatively impact species richness. **See also**: Interspecific Competition

Disturbance effects on competition

The intermediate disturbance hypothesis, initially proposed by Connell (1978), provides another explanation for species richness levels higher than those expected with competitive exclusion. It predicts low species diversity at both low and high levels of disturbance; at low levels, the most competitive species exclude others, while at very high levels of disturbance only a few species are able to survive the frequency or intensity of disturbance (**Figure 3**). Intermediate levels of disturbance are expected to maximize diversity (and thus species richness) because abundance of the most dominant species is reduced, allowing other species to establish, while at the same time not being so severe as to have the disturbance remove a significant number of species. For example, in pine savannahs on the coastal plain of the southeastern United States, disturbance from fires reduces the biomass of competitive shrubs that would otherwise cause reduced light levels at ground level. The light made available by fire allows a diverse suite of herbaceous species, including venus fly trap (*Dionaea muscipula*), to coexist. When fire is suppressed, shrubby species dominate, and the herbaceous species are shaded out.

Predation, pathogens, parasites and herbivores

Like disturbance, predation and herbivory can also regulate species richness within a system. Paine (1966) proposed the keystone species concept, where certain predators tend to exert an influence on the community disproportional to their abundance. Such predators typically provide top-down control over populations of prey species that might otherwise become dominant and exclude other species from the community. In the systems studied by Paine, starfish preyed upon dominant bivalve and barnacle species, reducing their populations and making space available for new species to occupy. When the starfish were

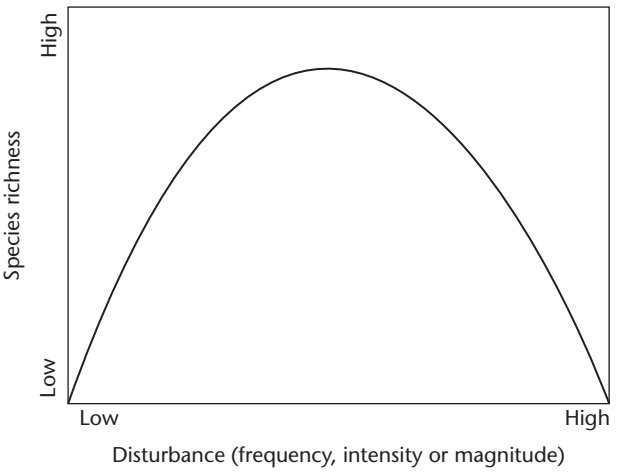

Figure 3 Illustration of the intermediate disturbance hypothesis about how disturbance affects species richness. Reprinted from Connell (1978) with permission from AAAS.

removed, the bivalves and barnacles increased in number, excluding other species from the sites and thereby reducing species diversity in those systems. Keystone species ranging from starfish in the intertidal to rabbits in grasslands can maintain small-scale species richness either by reducing organism size (and thus the asymmetry of competition), or by providing small gaps for establishment in what would otherwise be a uniformly competitive environment (maintaining intermediate levels of disturbance).

Interactions among pathogens, parasites and their hosts can also influence small-scale species richness. For species-specific pathogens and parasites, if adult individuals are able to withstand a greater parasite load than juveniles, then juveniles may experience higher rates of mortality close to conspecific, pathogen-carrying adults (Janzen, 1970; Connell, 1971). The high juvenile mortality adjacent to conspecific adults makes space available for less abundant species, thus increasing local species diversity. Pathogens and parasites that are less species-specific may increase coexistence of host species in the same way that predators can increase diversity by reducing the abundance of dominant species.

Facilitation

Facilitation occurs when the presence of one species helps the establishment and growth of other species, thus increasing species richness. For example, the presence of a nitrogen-fixing plant may allow other plant species to establish at a nitrogen-limited site. Similarly, 'nurse plants' provide otherwise rare conditions such as shade and soil stability in desert conditions, which allow other plants to establish and survive. Facilitating species may also create habitat that allows other species to persist in the community. One example of facilitation through habitat modification is the effect of *Spartina alterniflora* on coastal cobble beach communities. The *Spartina* beds stabilize the substrate of the cobble beach and create areas of substrate protected from wave action along the shoreline, allowing several rare plant species to persist and providing habitat for several invertebrate species (Bruno, 2000).

Facilitation may be complex and may occur over long periods of time. For example, in studies of primary succession at Mount Saint Helens, the presence of *Lupinus lepidus* inhibited the establishment of other species, but the seedlings of those species that were able to persist were more robust once the lupine senesced than they were in plots where no lupine was present initially (Morris and Wood, 1989).

Scale of observation may also affect interpretations of species interactions and their effect on diversity. Interactions that appear negative at one scale may actually be positive, increasing diversity when observed at a larger scale. For example, the primary space holding species studied by Paine (1966) appear to reduce local diversity of other sessile species if not held in check by keystone predators. However, recent evidence indicates that dominant space holding species increase community-wide diversity by creating unique areas of habitat utilized by a wide variety of species. Thus, at a community-wide scale, keystone species may actually reduce diversity (and thus species richness) by reducing the habitat diversity created by dominant species, such as mussel beds in aquatic systems (Bruno *et al*., 2003).

Environmental factors that affect species richness

Environmental gradients include both resource gradients such as water or soil nutrients for plants and gradients in conditions such as temperature and pH. Patterns of species richness across gradients depend on the interactions between individual species' ranges of tolerance and competition. Paradoxically, small-scale species richness is often low under environmental conditions that would be optimal for many species due to strong rates of interspecific competition. Thus, habitats with low resource levels (such as low nutrient soils for plants), moderate disturbance or moderately stressful conditions, often have high levels of small-scale species richness due to the effect of mitigated competition. The environmental variables that influence biological factors (such as competition, influenced by disturbance and resource availability) and geographic factors (such as propagule supply influenced by patterns of wind and water movement) will influence gradients of species richness.

Environmental heterogeneity can also contribute to local species richness by increasing γ diversity. Heterogeneous environments contain a broader array of conditions that may be optimal for a broader range of species than more homogeneous environments. For example, in some locations soil texture and nutrients can vary considerably over very small spatial scales, producing significant turnover in plant species richness through space. Similarly, topographic complexity creates considerable variation in temperature, moisture and other variables across a landscape, providing a wide variety of conditions for both plants and animals and therefore increasing the turnover in species richness across the landscape. **See also**: Environmental Heterogeneity: Temporal and Spatial

Temporal variation in small-scale species richness

As one evaluates the various factors that affect or are affected by species richness, it is important to remember that species richness varies through time as well as through space. Over long time scales, patterns of speciation and extinction influence species richness. Over shorter time scales, species richness is linked to geographic and environmental factors such as propagule availability, resource levels and disturbance which change through time. As Alexander Watt (1947) pointed out, communities are dynamic and patchy; they vary in time and space, and represent many patches in various stages of disturbance and recovery. As noted previously, disturbance can affect

species richness, as can immigration following disturbance. For example, succession describes the sequential changes in species composition that occur on new habitats, or following a disturbance (Clements, 1916; Keever, 1950). In most successional sequences, species richness increases over time as new species colonize the habitat, and then either remains stable or declines due to processes such as competition (Peet, 1992). In communities subject to repeated disturbances such as floods or fires, species richness may follow a pattern of rapid decline due to disturbance, then gradual increase for several years, followed by another disturbance and subsequent decline. Unfortunately, very few studies that measure small-scale species richness account for temporal variation. **See also**: Environmental Heterogeneity: Temporal and Spatial; Secondary Succession

Factors Affected by Species Richness

Productivity

While productivity is thought to affect species richness, with higher species richness at intermediate levels of productivity, it is also theorized that species richness can affect productivity. This may occur through several mechanisms including resource complementarity and facilitation. Resource complementarity occurs when species use resources in a complementary way (Hooper and Vitousek, 1997) maximizing the resources available for both species. For example, different species may require different nutrients, have different above or below ground space needs or grow at different times in the season, all of which allow for more complete and efficient use of resources and therefore greater production of biomass at a given site. Resource complementarity could have evolved in species occurring together for long periods of time to minimize resource competition. A second way richness may increase productivity is through facilitation, where the presence of one species, such as a nitrogen fixer, may increase the productivity of neighbouring species.

While experimental evidence has been found for species richness having a positive effect on productivity (Hector *et al*., 1999), the results have been controversial. An alternative explanation is a sampling effect, in which species-rich sites are more likely to include highly productive species (Aarssen, 1997), or species that act as facilitators. Ecologists have also been exploring the possibility that the positive effect of diversity on productivity seen in experiments is not due to species richness, but rather the number and identity of functional groups represented at a site (Hooper and Vitousek, 1997; Grime, 2002). Functional groups have traditionally been referred to as guilds, and are groupings of organisms based on shared characteristics such as morphology or similar resource use. For example, a site containing multiple functional groups such as nitrogen-fixing plants, forbs, graminoids and woody shrubs might have greater productivity than a site having more species but fewer functional groups represented.

Stability

Ecological stability can be measured in several ways, including the ability of a community to resist change (referred to as resistance and constancy), its ability to return to its original state following some form of perturbation (referred to as resilience), or the amount of variability in the community (Harrison, 1979). A widely held hypothesis is that greater diversity increases ecosystem stability, in part because more species-rich communities have a broader range of adaptations and can thus respond better to stress or disturbance (MacArthur, 1955; Elton, 1958). However, theoretical ecologists have suggested that more complex systems are less stable and more chaotic (May, 1972). More recently, ecologists have argued that the effect of diversity on stability depends on the measurement of stability used (e.g. resistance, resilience or variability may not react the same way), the amount of variability in the environment and the factors controlling diversity (Loreau *et al*., 2002; Thebault and Loreau, 2005). For example, strong interspecific interactions among species in diverse systems can lead to increased variability of individual populations, thus lower stability. However, because different species respond differently to environmental changes, increased species richness can buffer against environmental shifts (Loreau *et al*., 2002).

Invasibility

The ability of a community to resist invasion by nonresident species is a component of community stability. Species richness may reduce the invasibility of a community due to more complete use of resources (Elton, 1958). This has been supported by experimental evidence (Tilman, 1997), although results from field studies suggest that extrinsic ecological factors such as disturbance regime tend to have a greater effect on invasibility than species number per se, and tend to overwhelm any direct effect diversity has on invasibility (Foster, 2002). In addition, the scale of observation seems to affect whether the relationship is positive or negative. At small spatial scales, diversity appears to reduce invasibility, perhaps due to direct individual-to-individual competition occurring at small scales (Levine, 2000), or due to the inability to fit too many organisms into a small space (Fridley *et al*., 2004). However, at larger scales, the relationship between diversity and invasibility generally appears to be positive. This may be in part because processes that increase immigration, such as disturbance and high rates of seed input, seem to outweigh the effects of resource complementarity, causing high numbers of both native and exotic species (Levine, 2000; Brown and Peet, 2003). Note that at larger scales, exotic species richness is generally used as a measure of invasibility, while native species richness is used as a measure of diversity.

Conclusion

Efforts to understand patterns of small-scale species richness have provided a useful means through which to

examine how fundamental ecological processes affect local communities and have inspired a vast body of scientific research. Moreover, small-scale species richness can provide important information about the ecosystem. In systems where the processes affecting species richness are well understood, it can be used as an indicator of community properties such as resource availability or disturbance level, such as when diatom diversity is used to assess water pollution (Kutka and Richards, 1996). Understanding of the factors that influence species richness is particularly important for applying the concept to biodiversity conservation. The richest sites do not necessarily contain the rarest habitats, the highest levels of endemism or the species most threatened with extinction. Finally, it is important to remember that while species richness represents a relatively simple measure of diversity, the two are not the same. Species richness must always incorporate a scale of measurement; it is a species count per unit area, while diversity is a broader concept that attempts to account for the variety of life on Earth, not just of species but of all taxonomic levels and the functions, interactions and abundance of organisms.

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Further Reading

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